12

Are Some of the Recent Changes in Grassland Communities a Response to Rising CO₂ Concentrations?

H. Wayne Polley, Hyrum B. Johnson, Herman S. Mayeux, and Charles R. Tischler

I. Introduction

The abundance and density of C_3 trees and shrubs on predominantly C_4 grasslands in many parts of the world (Africa, Australia, North America, South America) have increased dramatically during approximately the last 125 years (reviews by Mayeux *et al.*, 1991; Archer, 1994). This rapid change in vegetation is evident from historical accounts and photographic records (Hastings and Turner, 1965) and repeated aerial photography (Archer *et al.*, 1988; Knight *et al.*, 1994) and censuses of permanent plots or similar areas (Glendening, 1952; Buffington and Herbel, 1965; Hennessy *et al.*, 1983), analyses of the stable carbon isotope composition of soil organic matter (Tieszen and Archer, 1990; Steuter *et al.*, 1990; McPherson *et al.*, 1993), and palynological evidence (Davis and Turner, 1986). Some woody species (e.g., *Prosopis glandulosa*, mesquite) apparently expanded within their historical ranges from refugia, like drainages or rocky outcrops that had been occupied for centuries, or increased in stature and visibility from suppressed populations (Bogusch, 1952; Johnston, 1963). For other species (e.g., *Larrea tridentata*, creosotebush), recent changes are an acceleration of an increase in density and range extension initiated centuries before (Hunziker *et al.*, 1977; Johnson and Mayeux, 1992). Production of grasses and other herbaceous species in many of these systems declines following woody ingress (Glendening, 1952; Heitschmidt and Dowhower, 1991;

Hobbs and Mooney, 1986), thus reducing the value of grasslands and savannas for livestock grazing and other uses. The shift in growth or life form composition also alters ecosystem-level processes, including surface–atmosphere transfers of matter and energy, that potentially influence rates and patterns of carbon sequestration (McPherson *et al.*, 1993; H. B. Johnson, unpublished data) and local, regional, or even global climates (Schlesinger *et al.*, 1990). By reducing grass production, for example, woody plants may lessen the frequency and intensity of fires and the accompanying return of carbon and nitrogen to the atmosphere (Medina, 1982; Hobbs *et al.*, 1991). By increasing spatial heterogeneity of soil water and nitrogen (Schlesinger *et al.*, 1990) or in other ways altering the hydrology of grasslands (Joffre and Rambal, 1993), woody ingress can change surface albedo, evapotranspiration, runoff, and fluxes of trace gases to the atmosphere.

Causes of the increase in abundance of woody plants have been extensively discussed because of the obvious importance of the change to economics and to longer term environmental concerns (e.g., Hastings and Turner, 1965; Grover and Musick, 1990; Bahre and Shelton, 1993; Archer, 1994). There is, however, relatively little experimental evidence documenting the cause or causes of woody invasion. Much of the evidence implicating specific causal factors in vegetation change is based on anecdotal accounts and is correlative and descriptive in nature.

Expansion of woody plants on grasslands has traditionally been attributed to rather site-specific changes, most of which increased recruitment or reduced the often size-dependent mortality of woody seedlings. These explanations include suppression of fire which often selectively kills woody seedlings (Bragg and Hulbert, 1976; Wright *et al.*, 1976), changes in the populations of rodents (Brown and Heske, 1990) which may both consume and disperse shrub seed and kill woody seedlings (Glendening and Paulsen, 1955; Gibbens *et al.*, 1992), changes in temperature or precipitation (Hastings and Turner, 1965; Neilson, 1986), removal of browsers (Belsky, 1984), and the effects of livestock introduced during the last 125 years (Bahre and Shelton, 1993; Archer 1994). Effects of livestock include the ingestion and dissemination of seed of some woody species (Glendening and Paulsen, 1955; Brown and Archer, 1987; Archer, 1989) and overgrazing that reduced grass production and the frequency of fires, reduced interference from grasses for light, water, and other resources (Bush and Van Auken, 1990), and may have increased spatial heterogeneity of soil nitrogen and water (Schlesinger *et al.*, 1990).

Each of these explanations for vegetation change is demonstrably important to some areas or for some species, but none of the traditionally advanced explanations for shrub encroachment satisfactorily explains the success of the diverse group of woody invaders across the diverse climatic and physiographic regions involved worldwide. Included are woody species

(e.g., *Acacia* spp., *Larrea tridentata, Juniperus* spp., *Prosopis* spp.) which differ greatly in potential growth rates, life histories, and tolerances to fire, drought, and shading, and grasslands on which precipitation differs markedly in seasonality, intensity, and predictability. Frequent fire alone probably was not sufficient to prevent invasion by *Prosopis,* for example, for it may not kill plants beyond the seedling stage (Wright *et al.,* 1976), but fire kills even large individuals of some *Juniperus* species and effectively limits or prevents invasion by these plants (Burkhardt and Tisdale, 1976). Conversely, seed dispersal by livestock greatly increased the rate and extent of grassland invasion by *Prosopis* (Brown and Archer, 1987; Archer, 1989) and perhaps other hard-seeded species, but cattle do not consume seed of *Juniperus* or *Larrea* and thus cannot have directly influenced dissemination of these plants.

Traditionally cited explanations for woody ingress sometimes also fail to explain the changes observed even in individual species. York and Dick-Peddie (1969), for example, concluded that heavy grazing increased the cover of *Prosopis* and other woody species in desert grassland in New Mexico, but *Prosopis* increases rapidly regardless of grazing regime (Glendening, 1952; Smith and Schmutz, 1975; Hennessy *et al.,* 1983). It is, of course, difficult to completely exclude prior effects of livestock and other factors in most studies, but similar increases in abundance have been noted in other woody species when grazing was absent (Rice and Westoby, 1978; Williams *et al.,* 1987).

Widespread encroachment of woody species on grasslands began shortly after atmospheric CO_2 concentration rose above its preindustrial level of 270–280 ppm. The global nature of the increase in CO_2, near synchrony of changes in CO_2 and vegetation, and multiple benefits of higher CO_2 to C_3 plant growth suggest that the historical rise in CO_2 concentration contributed to woody ingress. Higher CO_2 concentration, for example, decreases photorespiration (Sharkey, 1988; Johnson *et al.,* 1993a) and increases the quantum yield (Ehleringer and Björkman, 1977; Long and Drake, 1991) and temperature optimum of C_3 photosynthesis (Long, 1991). Rising CO_2 increases rates or amounts of N_2 fixation by woody legume–*Rhizobium* symbioses (Norby, 1987; Thomas *et al.,* 1991; Polley *et al.,* 1994) and often increases the nitrogen use efficiency and growth of woody (Norby *et al.,* 1986; Polley *et al.,* 1994) and other C_3 plants (Polley *et al.,* 1995a). Further, tolerance of C_3 plants to heat, drought, salinity, and other stresses is improved by higher CO_2 concentration (Idso, 1989). These and other changes may contribute to shift the competitive balance in favor of taller plants (Reekie and Bazzaz, 1989), possibly including C_3 shrubs over C_3 grasses, and of taller C_3 over co-occurring C_4 plants at elevated CO_2 (e.g., Bazzaz and Carlson, 1984; Arp *et al.,* 1993). The relative and, sometimes, absolute effect of a per-unit increase in CO_2 concentration on C_3 physiology

(Johnson *et al.*, 1993a; Polley *et al.*, 1993b) and growth (Polley *et al.*, 1992; Polley *et al.*, 1994) may be greater over the subambient levels indicative of the past than at future levels, suggesting that the historical rise in CO_2 concentration, albeit small (70–80 ppm), also generally favored greater production, taller vegetation, and taller C_3 over C_4 competitors (Fig. 1).

Clearly, there are instances in which competitive success at higher CO_2 concentrations is explained by factors other than or in addition to photosynthetic pathway (Bazzaz *et al.*, 1989). Results from CO_2-enrichment studies on C_4-dominated tallgrass prairie in Kansas, however, generally support the suggestion that taller C_3 plants may increase on grassland as CO_2 concentration rises. Owensby *et al.* (1993), for example, reported that basal cover of relatively tall and deep-rooting C_3 forbs on the prairie increased following a doubling of the current CO_2 concentration. Frequency (Nie *et al.*, 1992) and basal cover (Owensby *et al.*, 1993) of the shorter C_3 grass *Poa pratensis* declined in chambered plots exposed both to the current and elevated CO_2 concentration, though both frequency and basal cover declined less rapidly in plots fumigated with high CO_2 (frequency declined less rapidly at high CO_2 only when soils were well watered).

Increased widths of annular rings of some trees (LaMarche *et al.*, 1984; Hari and Arovaara, 1988) and greater C accumulation in temperate forests
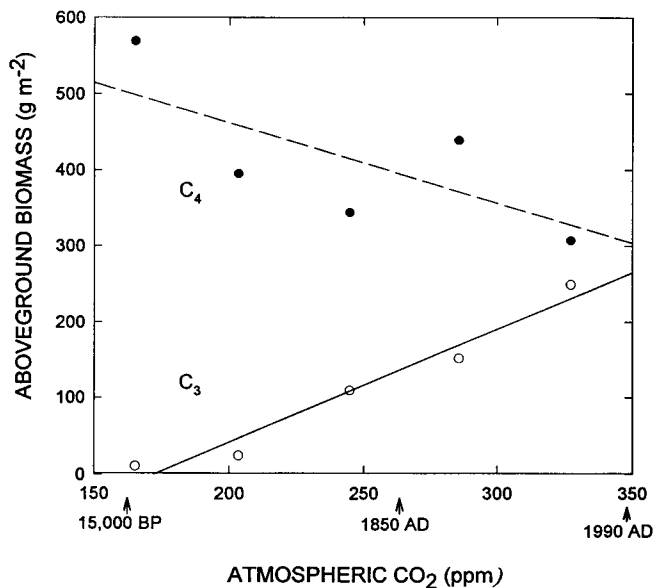
Figure 1   Aboveground biomass of C_3 and C_4 species that developed from the seed bank of a Texas savanna soil exposed for 13 weeks to a gradient in daytime CO_2 concentration from near 350 to 150 ppm. Figure reprinted from Johnson *et al.* (1993a). Reprinted with permission of Kluwer Academic Publishers.

(Kauppi *et al.,* 1992) in recent decades, suggest that the historical increase in CO_2 has stimulated growth of at least some woody vegetation. Woody plants also usually grow more rapidly when exposed to atmospheres enriched in CO_2, even when soil nutrients or water is limiting (Tolley and Strain, 1985; Norby *et al.,* 1986; Conroy *et al.,* 1990; Norby and O'Neill, 1991; Conroy *et al.,* 1992). Further, initial benefits of elevated CO_2 to growth of woody plants may be multiplied over time when environmental conditions are favorable (Idso *et al.,* 1991).

Resolving the role of rising atmospheric CO_2 concentration in the changing structure of grasslands and, more generally, in vegetation change is not straightforward. The dynamics of any species is the resultant of complex interactions among a number of factors, including its life history, physiology, and morphology, that vary in relative importance with the biotic and abiotic environments. Despite the difficulty and perhaps futility of attempting to assign a relative weight to livestock, fire suppression, climate change, rising CO_2, and other factors that contributed to vegetation change on grasslands and savannas, it remains important from a management perspective to identify when each of the potential contributors to change may be most influential. Here we briefly discuss what we perceive as the major obstacles to progress in identifying the relative contribution or importance of the historical increase in atmospheric CO_2 concentration to vegetation change on grasslands and savannas. Drawing largely from the vast and rapidly expanding literature documenting effects of elevated CO_2 levels on plants and ecosystems, we suggest mechanisms by which and conditions under which rising CO_2 may have contributed significantly to the observed increase in abundance of woody plants in many parts of the world.

II. CO_2 and Vegetation Change

Perhaps the greatest difficulty in experimentally defining how rising CO_2 influenced vegetation on grasslands results from inequities between the processes typically measured when CO_2 is varied and those most relevant to questions of vegetation change. Conjecture that CO_2 has contributed to a shift from mostly C_4 grasses to woody vegetation or from generally shorter to taller plants is based largely on physiological data and on observations that growth generally responds more positively to CO_2 in C_3 than C_4 plants (Poorter, 1993). The question of woody ingress, however, inherently is one of population biology or community ecology. Relevant processes at these levels include the life histories and morphologies, as well as physiologies, of species as influenced by biotic interactions and the abiotic environment. Most of the evidence that rising CO_2 concentration shifts the competitive balance in favor of C_3 over co-occurring C_4 species comes from experiments

with herbaceous plants in which competing species were planted nearly simultaneously and were of similar growth form or potential height and rooting depth (Bazzaz and Carlson, 1984; Arp *et al.*, 1993; Johnson *et al.*, 1993a). Competitive success in most of these experiments therefore was highly correlated with the response of growth rate or biomass production to CO_2. These data yield information on the likely responses of vegetation in highly disturbed habitats to CO_2, but have limited relevance to questions of change in established vegetation. Very little of the CO_2 work explicitly addressed the question of vegetation change in perennial systems in which invasive seedlings emerge in mature vegetation, a situation where the competitive success of seedlings will depend on their tolerance to resource depletion by neighboring adults (Goldberg, 1990), or competing plants differ in growth form. Of practical necessity, most CO_2 studies have been of limited duration and, with few exceptions (e.g., Bazzaz *et al.*, 1992; Morse and Bazzaz, 1994), have not considered possible feedbacks between growth responses of plants to CO_2 and the timing or magnitude of reproduction or other demographic parameters.

Can known physiological and whole-plant responses to rising CO_2 concentration be applied to predict the dynamics of grassland communities and responses of the diverse group of species involved? Linkages between physiology and populations or communities are inherently difficult to establish because relevant processes often differ among levels. When directed or guided by observations at community and population levels, however, physiological studies often may provide insight into those processes or periods during a plant's life cycle that are most critical to vegetation change. Vitousek (1993) similarly argued that recent success in applying physiological data to ecosystem-scale questions has resulted when physiological explanations were constrained by observations at higher levels.

Progress in identifying the contribution of rising CO_2 to the observed shift in grassland vegetation is further limited by the diverse biologies and life histories of woody invaders and by the wide range of environmental conditions that characterize invaded grasslands. When single species are considered or the spatial and temporal scales of observation are reduced to levels typical for most experimental evaluations, variation in the composition of vegetation increases and biotic and edaphic characteristics, local disturbances, past history, and annual weather variations strongly influence vegetation dynamics (Prentice, 1986). Not surprisingly, attempts to identify causal factors for vegetation change at these scales, even for single species, often yield contradictory results. General trends therefore are best sought at higher spatial and longer temporal scales.

## A. Interactions with Water Availability

It may prove useful to first approach the question of woody encroachment on grasslands at higher, perhaps regional, scales by identifying possible

interactions of CO_2 with mechanisms known to control the potential balance of trees or shrubs and grasses. At regional scales, climatic variables related to water availability and water balance appear most influential in controlling the potential distributions of vegetation types (Stephenson, 1990; Belsky, 1995) and their productivities (Sala *et al.*, 1988). Stephenson (1990), for example, demonstrated that actual evapotranspiration decreases and water deficit (evaporative demand not met by available water) increases along regional gradients in southern North America dominated first by forests, then by grasslands, and finally by shrublands (Fig. 2). Shrubs dominate the driest areas along the gradient either because they tolerate extreme soil and atmospheric drought or access deeply placed soil water not generally available to grasses. Because seedlings generally are more susceptible to drought than established individuals, however, woody establishment in these relatively arid environments is strongly correlated with rainfall and often occurs in pulses following large precipitation events (Turner, 1990). As water availability increases along this moisture gradient, production of grasses also increases. Woody seedlings can encounter severe interference from grasses for water and other resources in upper soil layers (Harrington, 1991). In some grasslands and savannas, therefore, the relative abundance of woody plants increases with increasing precipitation (Williams and Hobbs, 1989; Medina and Silva, 1990) and with soil or biotic factors that reduce water loss from surface soils and encourage accumulation in deeper layers (Knoop and Walker, 1985). In still more mesic areas, woody plants dominate at equilibrium apparently because they are superior competitors to shorter grasses for light (e.g., Tilman, 1988; Smith and Huston, 1989).
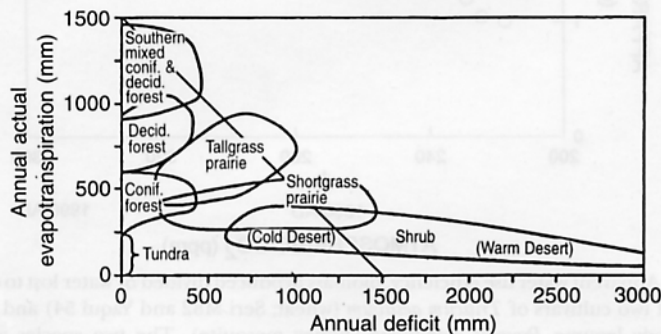
Figure 2   Mean annual evapotranspiration and annual deficit for major plant formations in North America (reproduced from Stephenson, 1990, with permission from the University of Chicago). Deficit is evaporative demand not met by available water. The diagonal connecting actual evapotranspiration of 1500 mm and deficit of 1500 mm depicts correlated changes in water balance and vegetation across an east-to-west transect of increasing aridity in the southern United States.

Atmospheric CO_2 directly affects the coupling between climatic water balance and vegetation by altering the efficiency with which plants use water, production per unit of transpiration (Fig. 3). At the leaf level, water use efficiency (WUE) often increases by about the same relative amount as does CO_2 concentration in both C_3 and C_4 species (Morison, 1993; Polley *et al.*, 1993a). Some of this potential increase in WUE may not have been realized by plants in nature if higher WUE was derived largely from lower transpiration. The decline in transpiration would have been partially offset by an accompanying increase in leaf temperature and a decrease in atmospheric humidity. For C_3 plants, however, much of the CO_2-mediated increase in WUE during the last 200 years apparently was realized as higher photosynthesis and greater biomass production (Polley *et al.*, 1993b; Polley *et al.*, 1994). Because of the strong correlation that exists between water availability and primary productivity in grasslands and deserts (Webb *et al.*,
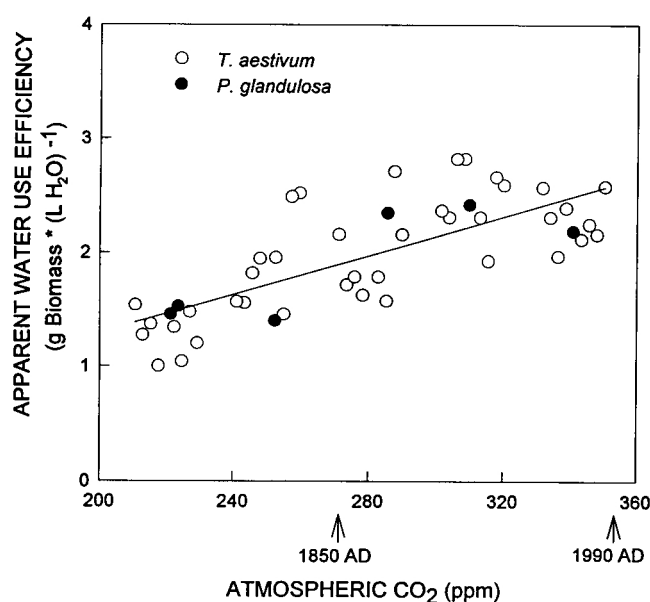
Figure 3   Apparent water use efficiency, biomass produced divided by water lost to evapotranspiration, of two cultivars of *Triticum aestivum* (wheat; Seri M82 and Yaqui 54) and individuals of the woody legume *Prosopis glandulosa* (honey mesquite). The two species were grown in separate experiments across daytime gradients in CO_2 concentration from near 350 to 200 ppm. Wheat was well-watered ($n = 20$) or droughted by withholding additional water for the last 50 days of the 100-day experiment ($n = 20$). *P. glandulosa* was droughted by adding water only after soil moisture had declined to 65% of volumetric content at field capacity for 9 of the 14 months of the experiment ($n = 6$). The line is a linear regression of water use efficiency on CO_2. Data are replotted from Polley *et al.* (1994) and (1995a).

1983; Sala *et al.,* 1988), the productivity of many grasslands should have increased substantially as atmospheric CO_2 rose. To the extent that rising CO_2 increases WUE and plant productivity, it also will increase potential leaf area and the potential for plant competition for light (Tilman, 1988; Smith and Huston, 1989). These changes, in turn, should favor taller growth forms like trees and shrubs at the expense of grasses, at least in relatively mesic grasslands.

By decreasing the amount of water required to sustain growth, the CO_2-mediated increase in plant WUE may also have increased survival of woody seedlings in more arid environments. Analyses of the carbon (C) isotope composition of aridland plants have shown that low values of leaf discrimination against ^{13}C (Δ), indicative of higher water use efficiency, are associated with greater plant longevity (Ehleringer and Cooper, 1988; Smedley *et al.,* 1991) and with greater survival during drought (Ehleringer, 1993). Projections based on changes in plant WUE also are compatible with observed effects of CO_2 on the C_3/C_4 composition of annual communities grown at different soil moisture levels (Bazzaz and Carlson, 1984). Characteristics like osmotic adjustment and the roots:leaves ratio that impact plant water balance and affect niche overlap among competing species may also have been altered as CO_2 rose (Miao *et al.,* 1992).

Rising CO_2 may also indirectly favor woody encroachment by decreasing transpiration rates of existing vegetation and thereby increasing soil water availability in grasslands and savannas (Polley *et al.,* 1995b). Shallow-rooting grasses are superior competitors to woody plants for water from upper soil depths. The abundance of deep-rooting trees and shrubs on some grasslands therefore depends on the amount of water that reaches soil below most grass roots (Knoop and Walker, 1985). When higher WUE derives largely from a decrease in transpiration per unit leaf area, as it often does in C_4 grasses, rising CO_2 will reduce the rate of soil water depletion provided the decline in transpiration per unit leaf is not offset by an increase in leaf area or leaf temperature. This change may in turn increase soil water content and favor greater percolation to depths where woody roots predominate. Higher leaf temperatures (Kirkham *et al.,* 1991) and, in years with below normal precipitation, greater leaf area (Owensby *et al.,* 1993) partly offset water savings expected on C_4-dominated prairie from a decrease in conductance and transpiration per unit leaf area at elevated CO_2 concentration. Still, Kirkham *et al.* (1991) found that as a result of a 7–15% decline in evapotranspiration, soil moisture levels in prairie to a depth of 2 m were consistently higher at elevated than at the current CO_2 concentration, even during periods of relatively severe drought (Owensby *et al.,* 1993).

B. Effects on Seedling Establishment and Growth

Population-level data for woody invaders and larger-scale studies of rates and patterns of woody ingress or expansion can be used to identify crucial

periods or processes during the life cycles of woody plants that may be most sensitive to CO_2 or to other factors. A seemingly trivial but important assumption implicit in attempts to identify factors that caused vegetation change is that woody populations were near equilibrium with grasses or were declining relative to grasses near the beginning of the 19th century. If woody populations were instead expanding, historical changes may simply have accelerated a vegetation change already predisposed under existing climatic conditions. Definitive data to judge the stability of woody/grass vegetation prior to the industrial revolution obviously are few and it must be recognized that a true equilibrium in vegetation composition is never attained (Johnson and Mayeux, 1992; Brown and Gersmehl, 1985). The assumption that woody populations were in equilibrium near the beginning of the 19th century appears reasonable for some species, but only approximately true for others. Archer (1989), for example, used a model of woody cluster development and age-size relationships to predict that most *Prosopis* plants in relatively mesic upland grassland/savanna in south Texas appeared since the late 1800s. Model results are consistent with other evaluations suggesting that the woody legume has only recently moved in great numbers onto grassland from refugia occupied perhaps for centuries (Bogusch, 1952). Abundance of creosotebush, like mesquite, has increased dramatically in former desert grassland during approximately the last 125 years (Buffington and Herbel, 1965). The recent increase in creosotebush, however, may be an acceleration of a process that proceeded for millenia. Creosotebush first appeared in quantity in the macrofossil record from the southwestern United States about 11,000 years ago. Johnson and Mayeux (1992) calculated that a subsequent expansion rate of about 16,000 ha/year was necessary to account for the distribution of creosotebush in the Chihuahuan, Sonoran, and Mojave Deserts. Johnson and Mayeux (1992) also discuss macrofossil evidence that blackbrush began to expand on these desert grasslands prior to European settlement. Similarly, Davis and Turner (1986) concluded from palynological data that expansion of *Juniperus* in Arizona began at least 2000 years before livestock were introduced. It appears then that changes during the historical period likely were not necessary to cause the ingress or expansion of some woody species. Changes apparently were, however, necessary to cause woody ingress or expansion onto grassland at the accelerated rates observed recently.

Given the relatively long life spans of many of the invasive species (Archer, 1994), the apparently limited changes in abundance of some woody species in the decades to centuries preceeding widespread and concentrated human intervention on grasslands and savannas implies that prior to the industrial revolution, seedling recruitment and subsequent survival to reproductive maturity did not greatly exceed that required to replace existing woody plants. Models, for example, suggest that factors such as fire slow,

but do not prevent, the eventual dominance over grasses by some woody species provided that over their life span established trees contribute more than one reproductive individual to the next generation (Hochberg *et al.,* 1994). Seed production of mature individuals or seedling establishment and survival must have been very low for those woody invaders that were not expanding greatly prior to the 19th century. By enhancing seedling establishment and survival and/or seed dispersal, recent changes likely also increased the rates at which previously expanding woody populations grew. Given the diverse biologies and life histories of the woody plants involved, including species that differ greatly in growth rates and susceptibility to fire and other agents of mortality, the implication is that some influential mechanism or more likely a combination of mechanisms prevented or limited seedling establishment and survival of woody plants on grasslands.

Not surprisingly then, most of the factors that traditionally are believed to cause or accelerate woody expansion or ingress either reduced the often size-dependent mortality of woody seedlings or enhanced woody establishment and growth by relieving water stress or by otherwise reducing interference from resident grasses or increasing the availability of soil resources. Grassland fires (Wright *et al.,* 1976) and herbivory by small mammals (Gibbens *et al.,* 1992), for instance, selectively kill small seedlings of the woody legume, *Prosopis.* Suppression of fire and reductions in small mammal populations during the last two centuries thus likely contributed to a marked increase in seedling survival of this species. Conversely, establishment rates of mesquite can be increased by grazing or mowing (Bush and Van Auken, 1990) or after severe drought in some grasslands (Hennessy *et al.,* 1983), apparently because these changes reduce interference from taller grasses for light or other resources. Rising CO_2 may similarly have enhanced woody recruitment and reduced seedling mortality by reducing the amount of resources that plants required in order to grow until largely uncoupled from interference with neighboring grasses and the primary causes of mortality. By increasing plant water and nitrogen use efficiencies and, in woody legumes, rates and amount of N_2-fixation, for example, rising CO_2 can reduce the amount of water and nitrogen that woody plants required from the soil. Increasing CO_2 may also greatly increase growth rates of individually grown or spaced plants of woody invaders and other C_3 plants (Polley *et al.,* 1994; Johnson *et al.,* 1993b), changes that should facilitate woody ingress following disturbance by reducing the period during which woody seedlings are most susceptible to mortality and to interference from neighboring grasses. Some woody seedlings minimize interference for water with neighboring grasses by rapidly extending their roots below those of most grasses (Brown and Archer, 1990; Bragg *et al.,* 1993), a process that would have been abetted by an increase in growth rate as CO_2 rose. There are situations, however, where effects of CO_2 on woody plants likely

were minimal. Seedling tolerance of shade potentially was improved by an increase in the quantum yield (Ehleringer and Björkman, 1977; Long and Drake, 1991) or decrease in the light compensation point of photosynthesis as CO_2 rose (Hand *et al.*, 1993; Polley *et al.*, 1993b), but existing information suggests these changes had little influence on the growth of shaded plants (Körner and Arnone, 1992; see Gloser, Chapter 21). Limited data also suggest that rising CO_2 concentration sometimes is of little benefit to the growth of C_3 shrubs confined to the same rooting volume as grasses (Polley *et al.*, 1994).

III. Conclusions

Available evidence suggests that effects of the historical increase in CO_2 likely were greatest in grasslands or for woody species in which water and, to a lesser extent, nitrogen limited woody establishment and early growth. Effects of CO_2 also may have been pronounced in situations where rising CO_2 significantly increased growth rates of woody seedlings. It is likely, therefore, that rising CO_2 interacted positively with disturbances like grazing and prolonged drought that reduced the cover and growth of grasses and their ability to compete with woody seedlings. Woody plants that grew more quickly were susceptible for a shorter time to mortality from fire and herbivory and more rapidly attained reproductive maturity. Even a small reduction in the age of first reproduction can greatly increase the reproductive output of an individual (Cole, 1954). Woody plants that grew faster also more quickly became large enough to significantly impact ecosystem dynamics in ways that can feed back to enhance woody ingress. Large woody plants, for example, shade neighboring grasses or shelter small mammals that feed on herbaceous plants (Hobbs and Mooney, 1986) and, in some systems, thereby reduce grass production and the frequency or local intensity of fire. Large shrubs, by concentrating and cycling nutrients and changing hydrological properties beneath their canopies, may increase spatial heterogeneity of water and nitrogen (Schlesinger *et al.*, 1990). These changes may feed back to reduce the production and establishment of grasses and enhance shrub regeneration. Large trees or shrubs also serve as foci for bird-dispersed seed of other woody species (Archer *et al.*, 1988). Rising CO_2 likely was less influential in vegetation change on grasslands where the growth of woody seedlings was strongly limited by light because of the highly size-asymmetrical nature of competition for this resource (Weiner, 1990; Bazzaz and McConnaughay, 1992).

Although it appears reasonable that a change in CO_2 would directly and indirectly affect the productivity and composition of grasslands and savannas, it is not obvious on what time scale this should occur. Atmospheric

CO_2 rose slowly during the 19th and early 20th centuries (Friedli *et al.*, 1986), and thus probably played little role in the initial phase of woody expansion (Archer, 1994). Further, there can be a lag of decades to centuries between shifts in atmospheric conditions and vegetation change (Davis, 1986) that probably would have limited how quickly effects of the recent rise in CO_2 became evident. The typical lag between cause and effect often results from the limited rates at which propagules disperse and the inertial resistance of established vegetation to change—the ability of perennial vegetation that established during favorable periods to persist under unfavorable conditions for decades without reproducing. The limit to change imposed by vegetative inertia may partly have been offset because of the highly asymmetric nature of competition between grasses and trees or shrubs that greatly favors the taller growth form when woody plants overtop grasses. Similarly, limitations of propagule dispersal were partly relieved for those species with seed that are disseminated by livestock. Still, effects of the near 30% increase in CO_2 during the last two centuries likely are not fully evident. Vegetation almost certainly is not in equilibrium with atmospheric CO_2, which presently is changing at an accelerated rate.

IV. Summary

The widespread and rapid increase in abundance and density of a diverse group of woody species on grasslands during the last two centuries likely is the result of several, often interrelated and reinforcing changes (Smeins, 1983; Belsky, 1990) including fire suppression, overgrazing, changes in rodent and browser populations, climate change, and the 30% increase in atmospheric CO_2 concentration. Rising CO_2 concentration, by increasing plant water use efficiency, increased potential production of vegetation in frequently water-limited grasslands and may, by reducing transpiration, have increased soil water availability and percolation to depths where woody roots predominate. In the absence of severe and repeated disturbance, these changes should in time have favored taller plants, such as trees or shrubs, at the expense of shorter grasses, consistent with patterns observed along natural gradients of precipitation or soil resource availability (Tilman, 1988). Given the lag of decades to centuries that often occurs between changes in atmospheric driving variables like CO_2 concentration and shifts in vegetation, it is highly unlikely that the potential response of vegetation to the historical increase in CO_2 concentration has been fully realized or that rising CO_2 alone was sufficient to account for the rates and patterns of woody ingress observed in some areas during approximately the last 125 years.

Effects of rising CO_2 concentration that were initiated during the past century or more should become increasingly evident with time and as CO_2 continues to increase during the foreseeable future. Because so little of the CO_2 work to date has addressed questions of vegetation change in perennial systems, experimentation in appropriate ecosystems is badly needed. To refine our understanding of the role of rising CO_2 in woody ingress on grasslands and in vegetation change generally, it also will be necessary to understand interactions between disturbances and the potential productivity of grasslands on the species and growth form composition of these communities. Progress in recent theoretical (Tilman, 1988) and empirical studies is evident (Wilson and Tilman, 1991). To predict likely effects of atmospheric changes on individual species, it also will be necessary to understand how CO_2 concentration affects environmental conditions under which species can grow and reproduce. Each stage in a plant's life cycle, from germination and establishment through vegetative growth and reproduction, potentially can be influenced directly or indirectly by atmospheric CO_2 concentration. Relevant processes or periods must be identified. Rates of woody expansion on grassland are highly sensitive to the number of reproductive plants that are recruited into the population from mature individuals (Hochberg *et al.,* 1994), suggesting that factors that altered seedling establishment and survival were critical to woody expansion. It is of particular importance in predicting vegetation change, then, to understand the interaction of CO_2 with seedling requirements for resources such as water that are likely to limit seedling establishment, survival, and growth. We suggest that rising CO_2 likely was most influential in those grasslands in which water or N limited woody recruitment and in which rising CO_2 significantly increased growth rates and the fecundity of woody plants. Ultimately, the ability to predict effects of rising CO_2 concentration on the dynamics of woody or other species requires an improved understanding of relationships between physiological and growth responses to CO_2 and the persistence of plant populations (Austin, 1992).

Acknowledgments

References

Archer, S. (1989). Have southern Texas savannas been converted to woodlands in recent history? *Am. Nat.* **134,** 545–561.

Archer, S. (1994). Woody plant enchroachment into southwestern grasslands and savannas: Rates, patterns, and proximate causes. *In* "Ecological Implications of Livestock Herbivory in the West" (M. Vavra, W. A. Laycock, and R. D. Pieper, eds.), pp. 13–68. Society for Range Management, Denver, CO.

Archer, S., Scifres, C., and Bassham, C. R. (1988). Autogenic succession in a subtropical savanna: Conversion of grassland to thorn woodland. *Ecol. Monogr.* **58**, 111–127.

Arp, W. J., Drake, B. G., Pockman, W. T., Curtis. P. S., and Whigham, D. F. (1993). Interactions between C_3 and C_4 salt marsh plant species during four years of exposure to elevated atmospheric CO_2. *Vegetatio* **104/105**, 133–143.

Austin, M. P. (1992). Modelling the environmental niche of plants: Implications for plant community response to elevated CO_2 levels. *Aust. J. Bot.* **40**, 615–630.

Bahre, C. J., and Shelton, M. L. (1993). Historic vegetation change, mesquite increases, and climate in southeastern Arizona. *J. Biogeogr.* **20**, 489–504.

Bazzaz, F. A., and Carlson, R. W. (1984). The response of plants to elevated CO_2. I. Competition among an assemblage of annuals at two levels of soil moisture. *Oecologia* **62**, 196–198.

Bazzaz, F. A., and McConnaughay, K. D. M. (1992). Plant–plant interactions in elevated CO_2 environments. *Aust. J. Bot.* **40**, 547–564.

Bazzaz, F. A., Garbutt, K., and Reekie, E. (1989). Using growth analysis to interpret competition between a C_3 and a C_4 annual under ambient and elevated CO_2. *Oecologia* **79**, 223–233.

Bazzaz, F. A., Ackerly, D. D., Woodward, R. I., and Rochefort, L. (1992). CO_2 enrichment and dependence of reproduction on density in an annual plant and a simulation of its population dynamics. *J. Ecol.* **80**, 643–651.

Belsky, A. J. (1984). The role of small browsing mammals in preventing woodland regeneration in the Serengeti National Park, Tanzania. *Afr. J. Ecol.* **22**, 271–279.

Belsky, A. J. (1990). Tree/grass ratios in East African savannas: A comparison of existing models. *J. Biogeogr.* **17**, 483–489.

Belsky, A. J. (1995). Spatial and temporal landscape patterns in arid and semi-arid African savannas. *In* "Mosaic Landscapes and Ecological Processes" (L. Hansson, L. Fahrig, and G. Merriam, eds.), pp. 31–56. Chapman & Hall, London.

Bogusch, E. R. (1952). Brush invasion in the Rio Grande plain of Texas. *Texas J. Sci.* **4**, 85–91.

Bragg, T. B., and Hulbert, L. C. (1976). Woody plant invasion of unburned Kansas bluestem prairie. *J. Range Manage.* **29**, 19–24.

Bragg, W. K., Knapp, A. K., and Briggs, J. M. (1993). Comparative water relations of seedling and adult *Quercus* species during gallery forest expansion in tallgrass prairie. *For. Ecol. Manage.* **56**, 29–41.

Brown, J. R., and Archer, S. (1987). Woody plant seed dispersal and gap formation in a North American subtropical savanna woodland: The role of domestic herbivores. *Vegetatio* **73**, 73–80.

Brown, J. R., and Archer, S. (1990). Water relations of a perennial grass and seedling vs adult woody plants in a subtropical savanna, Texas. *Oikos* **57**, 366–374.

Brown, D. A., and Gersmehl, P. J. (1985). Migration models for grasses in the American midcontinent. *Ann. Assoc. Am. Geogr.* **75**, 383–394.

Brown, J. H., and Heske, E. J. (1990). Control of a desert–grassland transition by a keystone rodent guild. *Science* **250**, 1705–1707.

Buffington, L. C., and Herbel, C. H. (1965). Vegetational changes on a semidesert grassland range from 1858 to 1963. *Ecol. Monogr.* **35**, 139–164.

Burkhardt, J. W., and Tisdale, E. W. (1976). Causes of juniper invasion in southwestern Idaho. *Ecology* **57**, 472–484.

Bush, J. K., and Van Auken, O. W. (1990). Growth and survival of *Prosopis glandulosa* seedlings associated with shade and herbaceous competition. *Bot. Gaz.* **151**, 234–239.

Cole, L. C. (1954). The population consequences of life history phenomena. *Q. Rev. Biol.* **29**, 103–137.

Conroy, J. P., Milham. P. J., Mazur, M., and Barlow, E. W. R. (1990). Growth, dry weight partitioning, and wood properties of *Pinus radiata* D. Don after 2 years of CO_2 enrichment. *Plant Cell Environ.* **13,** 329–337.

Conroy, J. P., Milham, P. J., and Barlow, E. W. R. (1992). Effect of nitrogen and phosphorus availability on the growth response of *Eucalyptus grandis* to high CO_2. *Plant Cell Environ.* **15,** 843–847.

Davis, M. B. (1986). Climatic instability, time lags, and community disequilibrium. *In* "Community Ecology" (J. Diamond and T. J. Case, eds.), pp. 269–284. Harper & Row, New York.

Davis, O. K., and Turner, R. M. (1986). Palynological evidence for the historic expansion of juniper and desert shrubs in Arizona, U.S.A. *Rev. Palaeobot. Palynol.* **49,** 177–193.

Ehleringer, J. R. (1993) Variation in leaf carbon isotope discrimination in *Encelia farinosa:* Implications for growth, competition, and drought survival. *Oecologia* **95,** 340–346.

Ehleringer, J., and Björkman, O. (1977). Quantum yields for CO_2 uptake in C_3 and C_4 plants. *Plant Physiol.* **59,** 86–90.

Ehleringer, J. R., and Cooper, T. A. (1988). Correlations between carbon isotope ratio and microhabitat in desert plants. *Oecologia* **76,** 562–566.

Friedli, H., Lötscher, H., Oeschger, H., Siegenthaler, U., and Stauffer, B. (1986). Ice core record of the $^{13}C/^{12}C$ ratio of atmospheric CO_2 in the past two centuries. *Nature* **324,** 237–238.

Gibbens, R. P., Beck, R. F., McNeely, R. P., and Herbel, C. H. (1992). Recent rates of mesquite establishment in the northern Chihuahuan Desert. *J. Range Manage.* **45,** 585–588.

Glendening, G. E. (1952). Some quantitative data on the increase of mesquite and cactus on a desert grassland range in southern Arizona. *Ecology* **33,** 319–328.

Glendening, G. E., and Paulsen, H. A., Jr. (1955). "Reproduction and Establishment of Velvet Mesquite as Related to Invasion of Semidesert Grasslands." United States Department of Agriculture, Forest Service Technical Bulletin 1127.

Goldberg, D. E. (1990). Components of resource competition in plant communities. *In* "Perspectives on Plant Competition" (J. B. Grace, and D. Tilman, eds.), pp. 27–49. Academic Press, San Diego.

Grover, H. D., and Musick, H. B. (1990). Shrubland encroachment in southern New Mexico, U.S.A.: An analysis of desertification processes in the American southwest. *Clim. Change* **17,** 305–330.

Hand, D. W., Warren Wilson, J., and Acock, B. (1993). Effects of light and CO_2 on net photosynthetic rates of stands of aubergine and *Amaranthus. Ann. Bot.* **71,** 209–216.

Hari, P., and Arovaara, H. (1988). Detecting CO_2 induced enhancement in the radial increment of trees. Evidence from northern timber line. *Scand. J. For. Res.* **3,** 67–74.

Harrington, G. N. (1991). Effects of soil moisture on shrub seedling survival in a semi-arid grassland. *Ecology* **72,** 1138–1149.

Hastings, J. R., and Turner, R. M. (1965). "*The Changing Mile.*" Univ. of Arizona Press, Tucson.

Heitschmidt, R. K., and Dowhower, S. L. (1991). Herbage response following control of honey mesquite within single tree lysimeters. *J. Range Manage.* **44,** 144–149.

Hennessy, J. T., Gibbens, R. P., Tromble, J. M., and Cardenas, M. (1983). Vegetation changes from 1935 to 1980 in mesquite dunelands and former grasslands of southern New Mexico. *J. Range Manage.* **36,** 370–374.

Hobbs, N. T., Schimel, D. S., Owensby, C. E., and Ojima, D. S. (1991). Fire and grazing in the tallgrass prairie: Contingent effects on nitrogen budgets. *Ecology* **72,** 1374–1382.

Hobbs, R. J., and Mooney, H. A. (1986). Community changes following shrub invasion of grassland. *Oecologia* **70,** 508–513.

Hochberg, M. E., Menaut, J. C., and Gignoux, J. (1994). The influences of tree biology and fire in the spatial structure of the West African savannah. *J. Ecol.* **82,** 217–226.

Hunziker, J. H., Palacois, R. A., Poggio, L., Naranjo, C. A., and Yang, T. W. (1977). Geographic distribution, morphology, hybridization, cytogenetics and evolution. *In* "Creosotebush:

The Biology and Chemistry of *Larrea* in New World Deserts" (T. J. Mabry, J. H. Hunziker, and D. R. DiFeo, eds.), pp. 10–47. Dowden, Hutchinson and Ross, Stroudsburg, PA.

Idso, S. B. (1989). "Carbon Dioxide and Global Change: Earth in Transition." IBR Press, Tempe, AZ.

Idso, S. B., Kimball, B. A., and Allen, S. G. (1991). CO_2 enrichment of sour orange trees: 2.5 years into a long-term experiment. *Plant Cell Environ.* **14,** 351–353.

Joffre, R., and Rambal, S. (1993). How tree cover influences the water balance of Mediterranean rangelands. *Ecology* **74,** 570–582.

Johnson, H. B., and Mayeux, H. S. (1992). Viewpoint: A view on species additions and deletions and the balance of nature. *J. Range Manage.* **45,** 322–333.

Johnson, H. B., Polley, H. W., and Mayeux, H. S. (1993a). Increasing CO_2 and plant–plant interactions: Effects on natural vegetation. *Vegetatio* **104/105,** 157–170.

Johnson, H. B., Polley, H. W., and Mayeux, H. S. (1993b). Elevated CO_2 amplifies expression of genetic variability in *Acacia smallii. Bull. Ecol. Soc.* **74,** 296.

Johnston, M. C. (1963). Past and present grasslands of southern Texas and northeastern Mexico. *Ecology* **44,** 456–466.

Kauppi, P. E., Mielikainen, K., and Kuusela, K. (1992). Biomass and carbon budget of European forests, 1971 to 1990. *Science* **256,** 70–74.

Kirkham, M. B., He, H., Bolger, T. P., Lawlor, D. J., and Kanemasu, E. T. (1991). Leaf photosynthesis and water use of big bluestem under elevated carbon dioxide. *Crop Sci.* **31,** 1589–1594.

Knight, C. L., Briggs, J. M., and Nellis, M. D. (1994). Expansion of gallery forest on Konza Prairie Research Natural Area, Kansas, USA. *Landscape Ecol.* **9,** 117–125.

Knoop, W. T., and Walker, B. H. (1985). Interactions of woody and herbaceous vegetation in a southern African savanna. *J. Ecol.* **73,** 235–253.

Körner, C., and Arnone, J. A., III. (1992). Responses to elevated carbon dioxide in artificial tropical ecosystems. *Science* **257,** 1672–1675.

LaMarche, V. C., Jr., Graybill, D. A., Fritts, H. C., and Rose, M. R. (1984). Increasing atmospheric carbon dioxide: Tree ring evidence for growth enhancement in natural vegetation. *Science* **225,** 1019–1021.

Long, S. P. (1991). Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO_2 concentrations: Has its importance been underestimated? *Plant Cell Environ.* **14,** 729–739.

Long, S. P., and Drake, B. G. (1991). Effects of the long-term elevation of CO_2 concentration in the field on the quantum yield of photosynthesis of the C_3 sedge, *Scirpus olneyi. Plant Physiol.* **96,** 221–226.

Mayeux, H. S., Johnson, H. B., and Polley, H. W. (1991). Global change and vegetation dynamics. *In* "Noxious Range Weeds" (L. F. James, J. O. Evans, M. H. Ralphs, and R. D. Child, eds.), pp. 62–74. Westview Press, Boulder, CO.

McPherson G. R., Boutton, T. W., and Midwood, A. J. (1993). Stable carbon isotope analysis of soil organic matter illustrates vegetation change at the grassland/woodland boundary in southeastern Arizona, USA. *Oecologia* **93,** 95–101.

Medina, E. (1982). Nitrogen balance in the *Trachypogon* grasslands of central Venezuela. *Plant Soil* **67,** 305–314.

Medina, E., and Silva, J. F. (1990). Savannas of northern South America: A steady state regulated by water–fire interactions on a background of low nutrient availability. *J. Biogeogr.* **17,** 403–413.

Miao, S. L., Wayne, P. M., and Bazzaz, F. A. (1992). Elevated CO_2 differentially alters the responses of coocurring birch and maple seedlings to a moisture gradient. *Oecologia* **90,** 300–304.

Morison, J. I. L. (1993). Response of plants to CO_2 under water limited conditions. *Vegetatio* **104/105,** 193–209.

Morse, S. R., and Bazzaz, F. A. (1994). Elevated CO_2 and temperature alter recruitment and size hierarchies in C_3 and C_4 annuals. *Ecology* **75,** 966–975.

Neilson, R. P. (1986). High-resolution climatic analysis and southwest biogeography. *Science* **232,** 27–34.

Nie, D., Kirkham, M. B., Ballou, L. K., Lawlor, D. J., and Kanemasu, E. T. (1992). Changes in prairie vegetation under elevated carbon dioxide levels and two soil moisture regimes. *J. Veg. Sci.* **3,** 673–678.

Norby, R. J. (1987). Nodulation and nitrogenase activity in nitrogen-fixing woody plants stimulated by CO_2 enrichment of the atmosphere. *Physiol. Plant.* **71,** 77–82.

Norby, R. J., and O'Neill, E. G. (1991). Leaf area compensation and nutrient interactions in CO_2-enriched seedlings of yellow-poplar (*Liriodendron tulipifera* L.). *New Phytol.* **117,** 515–528.

Norby, R. J., O'Neill, E. G., and Luxmoore, R. J. (1986). Effects of atmospheric CO_2 enrichment on the growth and mineral nutrition of *Quercus alba* seedlings in nutrient-poor soil. *Plant Physiol.* **82,** 83–89.

Owensby, C. E., Coyne, P. I., Ham, J. M., Auen, L. M., and Knapp, A. K. (1993). Biomass production in a tallgrass prairie ecosystem exposed to ambient and elevated CO_2. *Ecol. Appl.* **3,** 644–653.

Polley, H. W., Johnson, H. B., and Mayeux, H. S. (1992). Growth and gas exchange of oats (*Avena sativa*) and wild mustard (*Brassica kaber*) at subambient CO_2 concentrations. *Int. J. Plant Sci.* **153,** 453–461.

Polley, H. W., Johnson, H. B., Marino, B. D., and Mayeux, H. S. (1993a). Increase in C_3 plant water-use efficiency and biomass over glacial to present CO_2 concentrations. *Nature* **361,** 61–64.

Polley, H. W., Johnson, H. B., Mayeux, H. S., and Malone, S. R. (1993b). Physiology and growth of wheat across a subambient carbon dioxide gradient. *Ann. Bot.* **71,** 347–356.

Polley, H. W., Johnson, H. B., and Mayeux, H. S. (1994). Increasing CO_2: Comparative responses of the C_4 grass *Schizachyrium* and grassland invader *Prosopis. Ecology* **75,** 976–988.

Polley, H. W., Johnson, H. B., and Mayeux, H. S. (1995a). Nitrogen and water requirements of C_3 plants grown at glacial to present carbon dioxide concentrations. *Funct. Ecol.* **9,** 86–96.

Polley, H. W., Mayeux, H. S., Johnson, H. B., and Tischler, C. R. (1995b). Viewpoint: Implications of rising atmospheric CO_2 concentration for soil water availability and shrub/grass ratios on grasslands and savannas. Submitted for publication.

Poorter, H. (1993). Interspecific variation in the growth response of plants to an elevated ambient CO_2 concentration. *Vegetatio* **104/105,** 77–97.

Prentice, I. C. (1986). Vegetation responses to past climatic variation. *Vegetatio* **67,** 131–141.

Reekie, E. G., and Bazzaz, F. A. (1989). Competition and patterns of resource use among seedlings of five tropical trees grown at ambient and elevated CO_2. *Oecologia* **79,** 212–222.

Rice, B., and Westoby, M. (1978). Vegetative responses of some Great Basin shrub communities protected against jack-rabbits or domestic stock. *J. Range Manage.* **31,** 28–34.

Sala, O. E., Parton, W. J., Joyce, L. A., and Lauenroth, W. K. (1988). Primary production of the central grassland region of the United States. *Ecology* **69,** 40–45.

Schlesinger, W. H., Reynolds, J. F., Cunningham, G. L., Huenneke, L. F., Jarrell, W. M., Virginia, R. A., and Whitford, W. G. (1990). Biological feedbacks in global desertification. *Science* **247,** 1043–1048.

Sharkey, T. D. (1988). Estimating the rate of photorespiration in leaves. *Physiol. Plant.* **73,** 147–152.

Smedley, M. P., Dawson, T. E., Comstock, J. P., Donovan, L. A., Sherrill, D. E., Cook, C. S., Ehleringer, J. R. (1991). Seasonal carbon isotopic discrimination in a grassland community. *Oecologia* **85,** 314–320.

Smeins, F. E. (1983). Origin of the brush problem—A geographical and ecological perspective of contemporary distributions. *In* "Proceedings—Brush Management Symposium," pp. 5–16. Texas Tech Univ. Press, Lubbock, TX.

Smith, D. A., and Schmutz, E. M. (1975). Vegetative changes on protected versus grazed desert grassland ranges in Arizona. *J. Range Manage.* **28,** 453–458.

Smith, T., and Huston, M. (1989). A theory of the spatial and temporal dynamics of plant communities. *Vegetatio* **83,** 49–69.

Stephenson, N. L. (1990). Climatic control of vegetation distribution: The role of the water balance. *Am. Nat.* **135,** 649–670.

Steuter, A. A., Jasch, B., Ihnen, J., and Tieszen, L. L. (1990). Woodland/grassland boundary changes in the middle Niobrara Valley of Nebraska identified by $\delta^{13}C$ values of soil organic matter. *Am. Midl. Nat.* **124,** 301–308.

Thomas, R. B., Richter, D. D., Ye, H., Heine, P. R., and Strain, B. R. (1991). Nitrogen dynamics and growth of seedlings of an N-fixing tree (*Gliricidia sepium* (Jacq.) Walp.) exposed to elevated atmospheric carbon dioxide. *Oecologia* **88,** 415–421.

Tieszen, L. L., and Archer, S. (1990). Isotopic assessment of vegetation changes in grassland and woodland systems. *In* "Plant Biology of the Basin and Range" (C. B. Osmond, L. F. Pitelka, and G. M. Hidy, eds.), Vol. 80, pp. 293–321. Springer-Verlag, Heidelberg.

Tilman, D. (1988). "Plant Strategies and the Dynamics and Structure of Plant Communities," Vol. 26. Princeton Univ. Press, Princeton, NJ.

Tolley, L. C., and Strain, B. R. (1985). Effects of CO_2 enrichment and water stress on gas exchange of *Liquidambar styraciflua* and *Pinus taeda* seedlings grown under different irradiance levels. *Oecologia* **65,** 166–172.

Turner, R. M. (1990). Long-term vegetation change at a fully protected Sonoran desert site. *Ecology* **71,** 464–477.

Vitousek, P. M. (1993). Global dynamics and ecosystem processes: Scaling up or scaling down? *In* "Scaling Physiological Processes Leaf to Globe" (J. R. Ehleringer, and C. B. Field, eds.), pp. 169–177. Academic Press, San Diego.

Webb, W., Szarek, S., Lauenroth, W., Kinerson, R., and Smith, M. (1983). Primary productivity and water use in native forest, grassland, and desert ecosystems. *Ecology* **59,** 1239–1247.

Weiner, J. (1990). Asymmetric competition in plant populations. *Trends Ecol. Evol.* **5,** 360–364.

Williams, K., and Hobbs, R. J. (1989). Control of shrub establishment by springtime soil water availability in an annual grassland. *Oecologia* **81,** 62–66.

Williams, K., Hobbs, R. J., Hamburg, S. P. (1987). Invasion of an annual grassland in northern California by *Baccharis pilularis* ssp. *consanguinea. Oecologia* **72,** 461–465.

Wilson, S. D., and Tilman, D. (1991). Interactive effects of fertilization and disturbance on community structure and resource availability in an old-field plant community. *Oecologia* **88,** 61–71.

Wright, H. A., Bunting, S. C., and Neuenschwander, L. F. (1976). Effect of fire on honey mesquite. *J. Range Manage.* **29,** 467–471.

York, J. C., and Dick-Peddie, W. A. (1969). Vegetation changes in southern New Mexico during the past hundred years. *In* "Arid Lands in Perspective" (W. G. McGinnies and B. J. Goldman, eds.), pp.157–166. Univ. of Arizona Press, Tucson.